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Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the occipital cortex beyond human V1/V2

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In visual masking, visible targets are rendered invisible by modifying the context in which they are presented, but not by modifying the targets themselves. Here, we localize the neuronal correlates of visual awareness in the human brain by using visual masking illusions. We compare monoptic visual masking activation, which we find within all retinotopic visual areas, with dichoptic masking activation, which we find only in those retinotopic areas downstream of V2. Because monoptic and dichoptic masking are equivalent in magnitude perceptually, the present results establish a lower bound for maintenance of visual awareness of simple unattended targets. Moreover, we find that awareness-correlated circuits for simple targets are restricted to the occipital lobe. This finding provides evidence of an upper boundary in the visual hierarchy for visual awareness of simple unattended targets, thus constraining the location of circuits that maintain the visibility of simple targets to occipital areas beyond V1/V2.

binocular rivalry | consciousness | feedback | functional MRI | standing wave

The search for the neural correlates of consciousness requires the localization of circuits in the brain that are sufficient to maintain awareness. To this end, brain areas have been sought within the ascending visual hierarchy that correlate, or more importantly, fail to correlate, with visual perception (1–17). In visual masking illusions, a target is rendered invisible by the action of a mask that is either in the same eye as the target (monoptic) or in the opposite eye from the target (dichoptic). Dichoptic and monoptic masking are mediated by different circuits in the visual hierarchy in monkeys; dichoptic masking is first generated by the binocular circuits of the cortex, whereas monoptic masking is generated by subcortical as well as cortical circuits (16). Moreover, the strength of visual masking (both monoptic and dichoptic) builds up iteratively within the early visual system, so that it is possible for neurons of a given area to process both dichoptic and monoptic masking, but to different degrees (16). Masking illusions, and in particular the standing wave version of masking we used here, evoke reliable blood oxygen level-dependent (BOLD) signals that correlate with perception within human visual cortex (18, 19). Because the psychophysical strengths of monoptic and dichoptic masking are equivalent (16, 20), we can find the point in the ascending visual hierarchy in which monoptic and dichoptic masking activity are both extant and thus determine the first point in the visual hierarchy at which awareness of visibility could potentially be maintained. Previous to this level, target responses will not be well inhibited during dichoptic masking: if these prior areas were sufficient to maintain visual awareness, the target would be perceptually visible during dichoptic masking conditions.

Here, we mapped the retinotopic visual areas with functional MRI (fMRI) in human subjects, and measured the BOLD signal in response to monoptic and dichoptic visual masking within each subject's individually mapped retinotopic areas. Our results show that dichoptic masking does not correlate with visual awareness in area V1 but begins only downstream of area V2, within areas V3,

V3A/B, V4, and later. These results agree with previous electrophysiological results in monkeys using both visual masking and binocular rivalry stimuli (4, 5, 16), as well as with one fMRI study of binocular rivalry in humans (17).

Having determined the lower boundary in the visual hierarchy for the perception of visual masking of simple targets, we set out to determine whether there was also an upper boundary. We isolated the parts of the brain that showed both an increase in BOLD signal when nonillusory visible targets were displayed, as well as a decrease in BOLD signal when the same targets were rendered less visible by visual masking. Surprisingly, only areas within the occipital lobe showed differential activation between visible and invisible targets. Thus, the combined results of our experiments suggest that visual areas beyond V2, but within the occipital lobe, are sufficient to maintain our awareness of simple targets.

Materials and Methods

Psychophysics. Subjects ($n = 5$) were given a brightness matching task while in the magnet. The three target conditions [Target-Only, SWI (a visual masking illusion called “The Standing Wave of Invisibility”), and Control] were presented on the left half of the screen, whereas a luminance-adjustable Target-Only stimulus was presented on the right half of the screen. The bars along the vertical meridian were removed so that the left and right stimulus sets would not potentially mask each other. Each subject's task was to adjust the luminance of the adjustable Target-Only side to match the appearance of the target in the left half of the screen. Stimuli were black (lowest possible luminance from the display system) on a white background (maximal luminance). To generate the Target Visibility Rating, subject luminance ratings were inverted and normalized to between 0 and 1, where 1 was the highest possible visibility of a black target on the display system and 0 was the lowest possible visibility.

fMRI. Seventeen healthy right-handed volunteers (of both genders between the ages of 18 and 40) were used for the monoptic study, and 14 of these returned for the dichoptic study, which was carried out on a different day. All had normal depth perception and normal or corrected-to-normal visual acuity. Subjects were paid \$20 per session. Most subjects were scanned on 3 separate days, with one session each day: monoptic study, retinotopic mapping, and dichoptic study. To be clear: “monocular” means “with respect to one eye,” “monoptic” means “monocular” or “same in both eyes,” “binocular” means “with respect to both eyes,” and “dichoptic” means “different in the two eyes.” All of our stimuli were binocular, but, in monoptic conditions, both the target and mask were presented

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Abbreviations: BOLD, blood oxygen level-dependent; fMRI, functional MRI; SWI, standing wave of invisibility; TR, repetition time; ROI, region of interest.

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both the target and mask stimuli to evoke the greatest possible BOLD signal. Mono-optic fMRI sessions were also presented with a control condition (shown in Fig. 1A, for a total of four mono-optic conditions) in which the timing of the standing wave was altered so that the targets were visible. Because the perceptual strength of mono-optic masking is equivalent to that of di-optic masking (16, 20), psychophysical testing of the new SWI configuration was conducted with mono-optic stimuli only.

Fig. 1B shows the perceptual visibility of the target under the various target conditions. The results quantify the experience of the subjects: The targets in the Target-Only and Control conditions were highly visible although the target in the SWI condition was low in visibility (one-way ANOVA, $F = 37.62$, $R^2 = 0.8625$, $P < 0.0001$).

Upper Boundary for Masking of Simple Targets. Fig. 2A shows significant functional activation to the Target-Only condition (blue and yellow voxels; $P < 0.05$ corrected, random effects analysis), after subtracting the voxels that responded significantly in the Mask-Only condition ($P < 0.05$ corrected, random effects analysis). This region of interest (ROI) defines the subset of cortical voxels that responded well to the target but not to the mask. Voxels that constitute circuits responsible for the visibility of targets presumably lie within this target-responsive ROI. These visibility-correlated voxels should moreover generate greater BOLD response to target-visible rather than to target-invisible conditions. We measured the responses of the two orthogonal conditions: Control (target-visible) and SWI (target-invisible) to determine the voxels that could potentially contain the neural correlates of target visibility (yellow, $P < 0.01$ uncorrected, random effects analysis). We found that these target visibility-correlated (yellow) voxels overlapped a subset of the target-responsive (blue) voxels. In this initial comparison, we used uncorrected statistics to liberally specify all possible regions that could potentially correlate with target visibility, including those regions that may show spurious correlations. Despite our use of liberal thresholds, only the occipital cortex produced activation. This result suggested that the circuits that maintain the awareness of target visibility may be confined to the occipital cortex. We ascertained the statistical significance of the occipital localization by comparing the average Control (target-visible) BOLD response with the average SWI (target-invisible) BOLD response in target-responsive ROI voxels within and outside the occipital cortex. The difference between Control and SWI conditions within occipital ROI voxels was averaged, and statistical significance was verified (Fig. 2B; Wilcoxon signed rank paired two-tailed t test, $P = 0.0039$ corrected, random effects analysis). We tested nonoccipital ROI voxels with the same analysis (Fig. 2C) and found no significant difference.

Although significant target responses were found in virtually all visual areas of the cortex (Fig. 2A, blue and yellow), we found visibility-related effects only in the occipital cortex (Fig. 2A, yellow). These results suggest that awareness of simple unattended targets, such as those used in the SWI, is generated by circuits within the occipital cortex.

One alternative interpretation of this result is that, whereas there may be visibility-related activity in the occipital lobe, the absence of visibility-related activity in nonoccipital areas may be due to regional cerebral blood flow differences, which would constitute a null-result. We addressed this possibility by comparing the occipital versus nonoccipital BOLD responses with the combined nonillusory conditions (Target-Only and Mask-Only). Occipital BOLD responses to nonillusory stimuli (Fig. 2D, purple) were weaker than nonoccipital BOLD responses (Fig. 2D, green; Wilcoxon signed rank paired two-tailed t test, $P = 0.0001$ corrected, random effects analysis). Therefore, rather than having misinterpreted a null-result, we have instead underestimated the significance of our occipital localization findings.

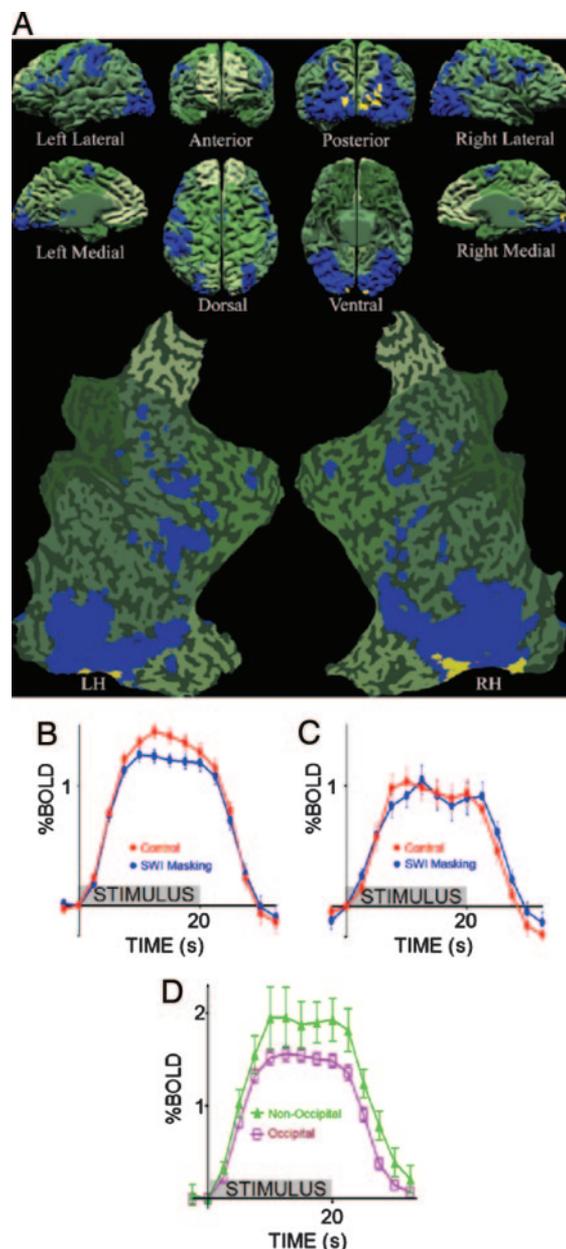


Fig. 2. Localization of visibility-correlated responses to the occipital lobe. (A) An individual brain model from all perspectives, including both hemispheres flat-mapped, overlaid with the functional activation from 17 subjects. The green shaded areas are those portions of the brain that did not show significant activation to Target-Only stimuli. The blue voxels exhibited significant target activation (Target-Only activation > Mask-Only activation). Yellow voxels indicate a significant difference found between Control (target-visible) and SWI (target-invisible) conditions, indicating potentially effective visual masking, and thus a correlation with perceived visibility. (B) Response time-course plots from Control versus SWI conditions in the occipital cortex (occipital masking). (C) Response time-course plots from Control versus SWI conditions in nonoccipital cortex (nonoccipital masking). (D) Response time-course plots from the nonillusory conditions (Target-Only and Mask-Only combined) in occipital versus nonoccipital cortex. (Error bars: (B, C, and D) SEM between subjects.)

Retinotopic Analysis. To study the visual hierarchy within the occipital lobe further, we used retinotopic analysis of the occipital visual areas (21), and delineated the ROIs for areas V1, V2v, V2d, V3v, V3d, V3A/B, and V4v in each of the subjects tested. Fig. 3 shows the retinotopic results from two subjects.

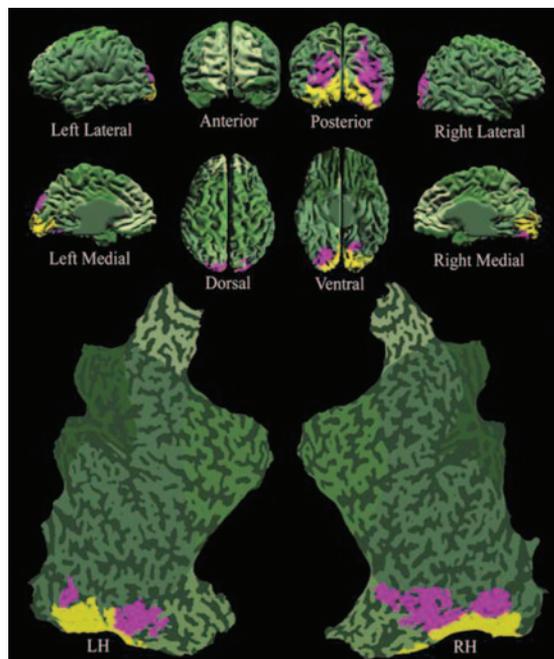


Fig. 5. Layout of retinotopic areas that potentially maintain awareness of simple targets. An individual brain model from all perspectives, including both hemispheres flat-mapped, overlaid with the functional activation from one typical subject. The yellow shaded areas are those portions of the brain that did not show significant dichoptic masking and thus are ruled out for maintaining visual awareness of simple targets (as in Fig. 4 *B* and *C*). The pink-colored voxels represent the cortical areas that exhibited significant dichoptic masking and thus are potential candidates for maintaining awareness of simple targets.

results also support the previous finding from monkey single-unit recordings that, whereas monoptic inhibition of the target begins to build up subcortically and achieves full strength in the binocular neurons of V1, dichoptic inhibition of the target does not begin until area V1 and therefore achieves full strength only after several iterations of inhibitory build-up within the extrastriate visual hierarchy (16).

Fig. 5 shows the layout of visual areas (downstream of areas V1 and V2) that could potentially maintain visual awareness of simple unattended targets (pink, matching shading in Fig. 4) in a single representative subject. V1 and V2 are colored in yellow (matching shading in Fig. 4).

Discussion

Implications for Binocular Rivalry as a Tool to Study Visual Awareness.

Binocular rivalry has been used as a tool to assess the neuronal correlates of visibility but has generated controversy because of conflicting results. Some fMRI studies on humans report that BOLD activity in V1 correlates with visual awareness of binocular rivalry percepts (11, 12). In contrast, other human fMRI studies (17), and single-unit recording studies in primates (5, 27), suggest that activity in area V1 does not correlate with visual awareness. One possible reason for this discrepancy is that none of the binocular rivalry studies have determined that the visual areas tested contained the interocular suppression circuits necessary to mediate binocular rivalry. That is, when binocular rivalry is not found in a given area, there is no extant method to control for the possibility that the circuits being studied simply do not have the components necessary to cause interocular suppression, and thus binocular rivalry. A more common conclusion is that the area cannot maintain visual awareness. However, if interocular suppression circuits do not exist in that area, then this conclusion would be

as inappropriate as concluding that V1 does not maintain awareness because it does not differentiate between houses and faces. Even when an indicator of neural activity in a given area is found to correlate with perceptual state during binocular rivalry, no existing study has determined whether the interocular suppression observed in that area is weak or strong. Until a control stimulus can be developed to indicate the strength of interocular suppression in any given area, unambiguous interpretation of the neural correlates of perceptual state during binocular rivalry will not be possible, no matter how high in the visual hierarchy. Thus, by using binocular rivalry stimuli alone, it is currently not possible to localize awareness circuits within the visual hierarchy.

In the present study, we measured the BOLD activity underlying visual awareness during monoptic and dichoptic masking in humans. With masking, one can compare the perceptual and neural strengths of both monoptic and dichoptic target suppression. This comparison supplies a means to quantify the strength of target suppression and also to determine whether a weak suppression of the target may be due to the weakness of interocular suppression in the circuit tested, or to the lack of masking components within the circuit.

Implications for Lateral Inhibition Models of Visual Masking.

Macknik and Martinez-Conde (16) previously recorded the responses of single neurons in the lateral geniculate nucleus (LGN) and primary visual cortex (V1) of awake monkeys to monoptic and dichoptic forms of the SWI illusion, and found that neither LGN nor V1 responses correlated with perception of dichoptic targets. To investigate the role of specific areas within the human occipital lobe in maintaining awareness, the present study mapped the retinotopic regions of the occipital lobe of each subject and then presented the SWI illusion monoptically and dichoptically to compare the responses in the retinotopic visual areas. Because monoptic and dichoptic visual masking are perceptually equivalent in magnitude (16, 20), only those areas with equivalent BOLD activity in monoptic and dichoptic masking conditions can potentially maintain visual awareness. Our results show that target suppression during monoptic masking is strong in all retinotopic occipital areas, but dichoptic masking builds up within the visual cortex and becomes strong only downstream of both dorsal and ventral V2 (i.e., within areas V3v, V3d, V3A/B, and V4v). These findings match previous primate single-unit recording results for area V1 (16), suggesting that area V1 plays a similar role in monkey and human visual awareness.

The ubiquitous strength of monoptic masking in the occipital retinotopic areas and the build-up of dichoptic masking strength in the extrastriate visual hierarchy are both predicted by the previous discovery that lateral inhibition builds up iteratively within the early visual system (16, 28). Unlike monoptic lateral inhibition, which begins in the retina and builds up to full strength in the striate cortex, lateral inhibition between the eyes (interocular suppression) begins to develop only in the binocular circuits of the striate cortex, and we show here that it does not reach full strength until the areas V3A/B and V4v (which may be hierarchically equivalent levels in the respective dorsal and ventral visual processing streams). We suggest that there are both lower and upper bounds within the visual hierarchy for the processing of visual masking and the maintenance of visual awareness of simple unattended targets; the lower bound is at least as high as the border between V2 and V3, and the upper bound is within the occipital lobe, possibly somewhere downstream of V4.

The dichoptic masking results are consistent with previous conclusions drawn from recordings in primates using binocular rivalry stimuli (27), in which perception-correlated processing was concluded to begin in the visual hierarchy as late as area V4. A later fMRI study conducted with motion-based rivalry in humans furthermore supports the idea that motion-based rivalry could not be maintained until human area V3A (17). Therefore, our current results, which suggest that visual awareness may be processed as

